

PHYSIOLOGICAL AND ECOLOGICAL STUDIES ON THE BIVALVE
MOLLUSK *ARTHRODONTA BIFURCA* (WEBSTER, 1908) LIVING
COMMENSALLY WITH THE TUBICOLOUS POLYCHAETE
PECTINARIA AUSTRALIS EHLERS, 1905

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Known commensal bivalves from New Zealand waters are the galeommatid *Scintillona zelandica* (Odhner) described in association with the synaptid holothurian *Trochodota dendyi* by Morton (1957), *Coriarcus neozelanicus* Dell (Leptonidae) recorded by Dell (1963) as attached to a new species of the echinoid genus *Cyclaster* in deep water, and two species of the leptonid genus *Arthritica*. *A. crassiformis* Powell is found living with the large rock-boring pholad *Anchomasa similis* (Gray), and *Arthritica hulmei* Ponder lives in association with the sea-mouse *Aphrodita australis* Baird. The biology and commensal relationships of these two species of *Arthritica* have been described by Ponder (1965).

The third New Zealand species of the genus *Arthritica*, *A. bifurca* (Webster), was considered by Ponder (1965) to be free-living before I noted its association with *Pectinaria australis*.

I would like to thank Professor J. E. Morton and Mr. W. F. Ponder for co-operation in this work, and Drs. R. K. Dell and R. B. Pike for constructive criticism of the manuscript.

SEASONAL VARIATIONS IN *PECTINARIA AUSTRALIS* AT PETONE BEACH (Fig. 3)

The tidal rise and fall at Petone Beach is 4.5 feet (1.37 meters) at spring tides which at low water uncover the sand for a distance of approximately 50 m.

Pectinaria australis is found at the high water neap tide level and occurs down to low water spring tides, but may extend below this level. *P. australis* lives within a conical tube of cemented sand grains in fine muddy sand. The broader anterior end of the tube is directed downwards and the narrow posterior end lies near the surface of the sand (Fig. 1). The location of *P. australis* on the exposed sand surface is usually indicated by a characteristic small exhalant hole one or two millimeters in diameter. In the aquarium, *P. australis* showed no evidence of a secondary inhalant hole in the sand near the tube, as illustrated for *P. koroni* by Watson (1928, p. 31, Fig. 2) but draws the inhalant current from around the sides of its tube as shown in Figure 1.

Samples were taken at low tide during the third week of each month between April, 1964, and March, 1965. Preliminary sampling showed *Pectinaria* to have a very patchy distribution. The position of these patches or "beds" on the beach

Fig. 1

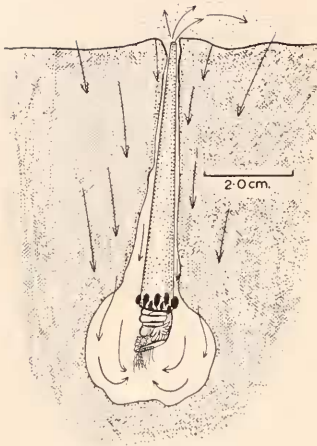


Fig. 2

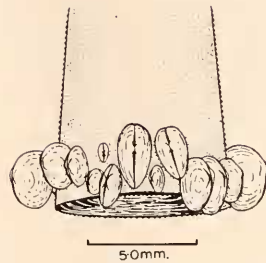


Fig. 3

Seasonal Distribution of *Pectinaria australis* on Petone Beach 1964-65

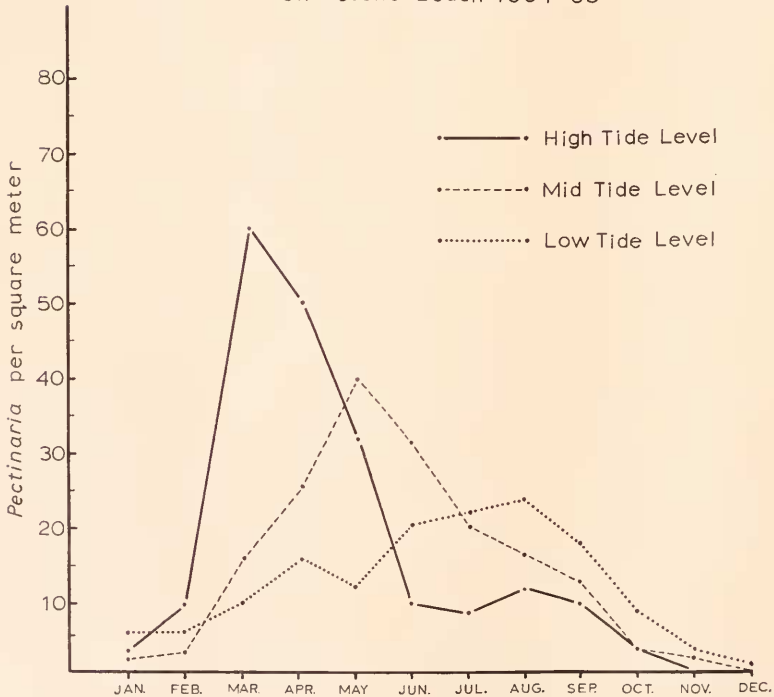


FIGURE 1. *Pectinaria australis* burrowing in aquarium sand. Water currents indicated by arrows. *Arthritica* shaded in solid black.

FIGURE 2. Position and orientation of *Arthritica bifurca* on *Pectinaria* tube.

FIGURE 3. Seasonal distribution of *Pectinaria australis* on Petone Beach. Based on data from samples: April, 1964, to March, 1965.

moved considerably, and transects were made through these areas wherever they occurred. Quadrats of one meter square and about 15 cm. deep were taken at 5-m. intervals from the high water neap tide level down the beach on the selected transects.

The *Pectinaria* population varied in density throughout the year, as shown by Figure 3. The extremely dense population which occurred at high tide level during March and April (autumn) comprised immature worms (tube length 10 mm. to 20 mm.) and appeared to be a separate population from the smaller numbers of much larger adult worms (tube length 35 mm. to 75 mm.) found at lower tide levels during these two months.

In May and June (early winter) the highest densities occurred around mid tide level, and were mainly immature worms (tube length 10 mm. to 35 mm.) while the smaller adult population still occupied the lower tide level. From July through to February the *Pectinaria* community could not be separated into two groups, as all worms were mainly mature and ranged in tube length between 40 mm. and 75 mm. During September and October (spring) the population density at all tide levels fell appreciably until November, December and January, when *Pectinaria* became very rare over the entire beach.

The extremely high numbers of immature worms found during March and April (Fig. 3) suggest that the main larval settlement occurred on the upper beach probably during February. During May and June the upper level population density fell sharply, but the numbers of young worms increased significantly at the mid tide level. As these worms had not increased in length from March they could have been derived from a later settlement and not by downward migration from the upper beach. The less pronounced population increase at low tide level shown during June, July and August could be similarly explained. Thus, the apparent migration of worms down the beach is probably due to mortality among the upshore and earlier settled population rather than to actual movement of the community down the beach.

Hence, with the community decreasing numerically from March through to the following February (Fig. 3) and the worms showing a marked length increase during this time, it is possible that *P. australis* lives for only 12 or 18 months and is subject to an extremely high mortality rate during growth and maturation and also after breeding in the spring. It is also probable that the population is replenished mainly during late summer by settlement of larvae at or near the high tide level, but there is evidence of a fairly extended breeding period.

No study was made of the possible causes for the patchy distribution of *Pectinaria* on Petone Beach. This may be due to gregarious tendencies in the planktonic larvae (Knight-Jones, 1951a, 1951b; Knight-Jones and Stephenson, 1950) or to the patchy occurrence of micro-organic food on the sand grains (Wilson, 1955). Mechanical sand grain analysis similar to the work of Pike and Le Sueur (1958) was not undertaken as there was no visible change in sand grain size in the transect areas.

ASSOCIATION OF *ARTHROITICA BIFURCA* WITH *PECTINARIA AUSTRALIS*

Arthritica bifurca is attached by several fine byssus threads to the outer surface of the head-end of the tube of *Pectinaria australis*, orientated vertically with its

anterior end directed downwards (Fig. 2). The bivalves were not found inside the tube of the worm and were rarely further than three millimeters from the anterior rim. Two specimens were found, however, attached to the sides of the burrows of *Abarenicola pacifica* (N. Z. lugworm). Ponder (1965) found occasional unattached specimens of *Arthritica bifurca* alive under stones at Auckland, New Zealand. Ponder (personal communication) also found the species living in mud at or below low tide level in the Auckland area where *Pectinaria* occurs, but the bivalves were not observed attached to the worm tubes. However, these samples were collected by dredging and sieving, and the bivalves may have become detached.

From the total numbers of polychaetes and bivalves observed at Petone Beach over the year only 10% of mature worms (tube length greater than 35 mm.) were without *Arthritica bifurca*, and those worms with bivalves carried between one and 22. It was not possible to determine the size range of *A. bifurca* throughout the year or to correlate the size of worm tube with the number of associated bivalves at different tide levels and seasons, owing to extreme variation in these factors—as found by Ponder (1965) in *A. crassiformis*. However, more *Arthritica* were associated with each worm, together with a higher incidence of association on the upper shore, than at lower tide levels.

The color of *Arthritica* changed progressively from creamy-white below the mid tide level through to brick-red or orange-black at the upper limit of its range. This is probably due to leaching and ferric oxide deposition which is quite common among the Leptonacea and other small bivalves.

ORIENTATION OF ARTHRITICA TO HOST

Experiments with living specimens were carried out at the Zoology Department's Marine Station at Island Bay, Wellington. As neither *Arthritica* nor *Pectinaria* occurs in the vicinity of the Marine Station, the laboratory sea-water supply had not come in contact with either animal prior to the experiments. To eliminate errors arising from possible phototactic responses in *Arthritica* all experiments were carried out in a darkened room.

The laboratory experiments were designed to determine: (1) If, in *A. bifurca*, there was any response to the presence of *Pectinaria australis* when the two species were separated in an aquarium. (2) The nature and degree of this response (if present) and to what extent *Arthritica bifurca* could distinguish between a water current from the host and a control current which had not come in contact with the host species.

A. bifurca moves with a gliding motion similar to that described for *A. crassiformis* by Ponder (1965). However, large numbers of *A. bifurca* in a dish of sea water moved neither rapidly nor at all constantly, and did not show mutual attraction resulting in the formation of clusters of individuals, as shown by the non-commensal *Lasaca rubra* (Eulamellibranchia, Erycinacea) under similar conditions (Morton, 1960).

As the moving polychaetes were found to leave a readily traceable furrow in fine compacted black sand brought from Petone Beach, it was not necessary to use the "talcum powder" technique suggested by Morton (1962).

Experiments were carried out using bivalves ranging from 0.40 mm. to 4.25 mm. in shell length.

Investigation 1 (Fig. 5)

(a) *Response to host stimulus*

A living *Pectinaria* was placed in a 7.5 cm. \times 2.5 cm. glass vial filled with sand. With the mobility of the animal thus restricted the vial was sunk in the center of a 46 cm. \times 28 cm. clear plastic tank containing about 10 cm. of fine sand and filled with fresh sea water. Two bivalves were placed on the surface of the sand in each of the four corners of the tank, and the experiment was left in a dark room for 12 hours. The water was in no way aerated or renewed.

The furrows left in the sand by moving bivalves were traced for each of five runs. A tracing of the fourth run in this series is shown in Figure 5. On three occasions all eight *Arthritica* located *Pectinaria* and on two occasions all but one of the bivalves were found on the rim of the tube.

(b) *Speed of movement*

In dim red light a similar system was set up, and with the aid of a stop-watch bivalves were timed as they moved towards the host. At two-minute intervals the distance travelled was recorded by measuring the length of the sand furrows with dividers. The distance travelled per second by moving *Arthritica* was calculated for each two-minute period. Bivalves 15 cm. to 20 cm. from *Pectinaria* (measured in a direct line) moved at 0.08 cm. per second, but within 5 cm. of the host this rate was increased to 0.20 cm. per second.

Interpretation

This investigation established that *Arthritica bifurca* is attracted to the exhalant currents of *Pectinaria*. Figure 5 also illustrates that the closer the bivalves get to the worm tube the more direct is the route taken, implying that the attractive force increases with proximity to its source. Close to *Pectinaria* the increased rate of movement shown by *Arthritica* is a direct orthokinetic response. However, there was no evidence of a consistent klinokinetic response. In some cases the rate of change of direction decreased nearer to the host, but in others it did not, and therefore no general pattern could be established.

Investigation 2

Random choice of host (Table I)

A 46 cm. \times 28 cm. clear plastic tank containing about 10 cm. of sand was filled with sea water. Fifty bivalves, and five tube worms, ranging between 20 mm. and 70 mm. in tube length, were scattered on the surface of the sand and left for 12 hours in a dark room. The water was not aerated or renewed. This experiment was carried out 10 times using different specimens of *Arthritica* and *Pectinaria* on each occasion. The percentage of bivalves found on the rim of a

Fig. 4

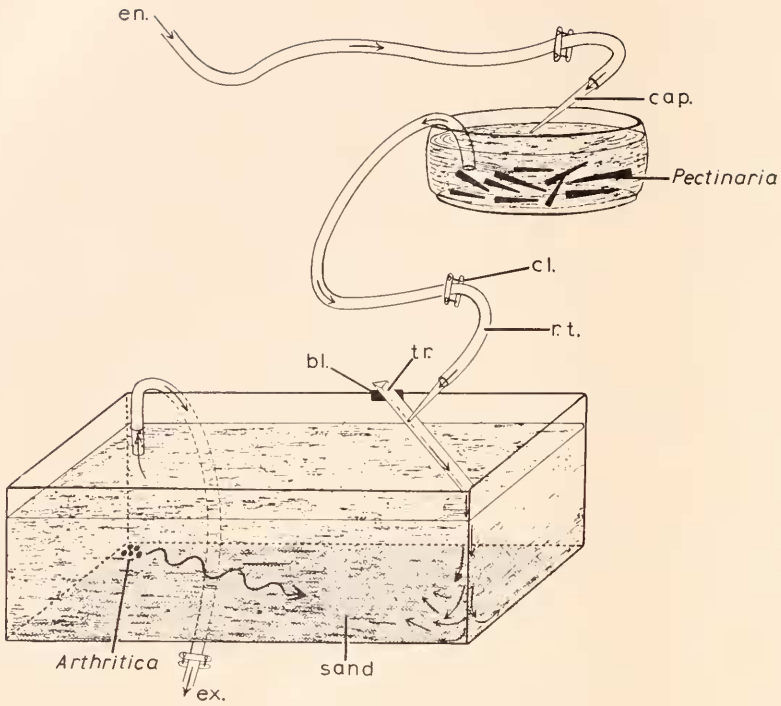


Fig. 5

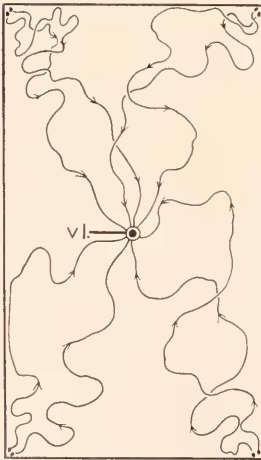


Fig. 6

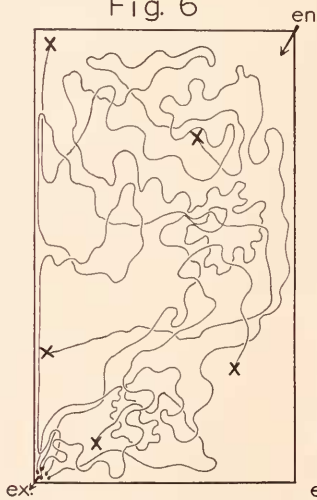


Fig. 7

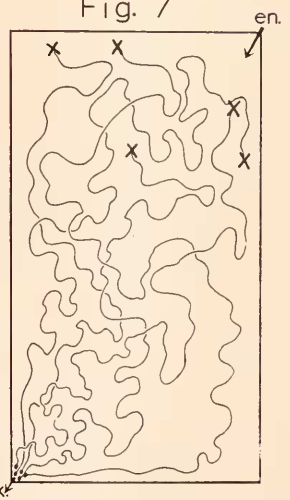


FIGURE 4. Diagram of apparatus used in Investigation 3: bl, wooden block; cap., capillary tube; cl., clamp; en., sea water entry; ex., sea water exit; r. t., rubber tubing; tr., trough. Direction of water flow indicated by arrows. General direction of *Arthritica* migration indicated by waving line.

TABLE I

Investigation 2—Percentage of *Arthritica* found in association with *Pectinaria* after 12 hours

Run No.	1	2	3	4	5	6	7	8	9	10
% success	90	92	86	88	96	98	82	86	90	88

Pectinaria tube after 12 hours is shown in Table I. After each run no more than 15 bivalves were found on any one tube.

Interpretation

An average of 90% *Arthritica* located *Pectinaria* in each experiment. This high figure suggests that there is probably some important, but as yet undiscovered, biological reason for its association with *Pectinaria*. Bivalves were found around the rims of all sizes of worm tube in approximately equal numbers, showing that *Arthritica bifurca* has no preference for *Pectinaria* of any specific size.

As *Pectinaria australis* is the only representative of the family Pectinariidae known from New Zealand, it was not possible to run a control experiment to determine host specificity.

Investigation 3

Response to host and control currents (Figs. 4, 6, 7)

The experiment was set up as shown in Figure 4, with balanced inflow and outflow of sea water. Inflowing water passed through a bowl containing 10 *Pectinaria* and then descended down one corner of the tank (en.) and was led out at the diagonally opposite corner (ex.). In this tank five bivalves were placed at the outflow end. The experiment was carried out five times in a dark room, each time with a control experiment having no *Pectinaria* in the inflow bowl. The first three runs were of 12 hours duration, but these resulted in an extremely complex trail pattern. Figures 6 and 7 are tracings of the fifth and final run of both the live and control experiments in which the running time was two hours.

Interpretation

The flow of water over the sand was rather diffuse and this resulted in *Arthritica* taking a less positive direction than might have been the case in a different assembly. Nevertheless there is a definite tendency for *Arthritica* to migrate towards the inflow corner when *Pectinaria* is present in the inflow current (Fig. 7), compared with a rather unoriented trail pattern with no definite evidence of rheotaxis shown

FIGURE 5. Investigation 1: Tracing of run no. 4. vl., glass vial containing *Pectinaria*.

FIGURE 6. Investigation 3: Tracing of 5th and final control run. Position of *Arthritica* after two hours indicated by "X." en., sea water entry; ex., sea water exit.

FIGURE 7. Investigation 3: Tracing of 5th and final live run. Position of *Arthritica* after two hours indicated by "X." en., sea water entry; ex., sea water exit.

by the control (Fig. 6). The presence of *Pectinaria* therefore causes chemotaxis of *Arthritica* towards the source of inflowing water.

DISCUSSION

Significant work has been published concerning species of the polynoid genera *Arctonoë*, *Acholoë*, *Gattyana*, *Lepidasthenia*, *Polynoë*, *Harmothoë* and *Halosydna*, and the physiology of their commensal relationships with their respective marine invertebrate hosts, by Davenport (1950, 1953a, 1953b) and by Davenport and Hickok (1951). Morton (1962) has shown that *Montacuta ferruginosa* is chemotactically attracted to its heart-urchin host. Conclusions drawn from experimental work in this paper support in principle that marine commensals are capable of finding their way to a specific host by chemotaxis.

Ponder (1965) has discussed biological advantages for *Arthritica crassiformis* in its association with *Anchomasa similis*, but could find no benefits for the pholad. Similarly, I could find no advantages for *Pectinaria australis* in its association with *Arthritica bifurca*. *Pectinaria* without bivalves attached appeared to be unaffected by their absence. Also, advantages for *Arthritica bifurca* appear to be even more obscure than those suggested by Ponder for *A. crassiformis*, as little protection is provided by the rather temporary worm burrow in the sand. The necessity for a commensal mode of life and the biological reasons for commensalism in the genus *Arthritica* are unknown.

Ponder has pointed out that leptonacean bivalves, by virtue of their small size, efficient mobility, temporary byssus fixation and larval incubation, are particularly adapted to a commensal mode of life with burrowing animals. Ponder has removed shelled prodissoconch larvae from adults of *A. crassiformis* and *A. hulmei* but it is not known at what stage of development larvae are released, or if in fact they are free-swimming on liberation. During March and April large numbers of prodissoconch larvae were found in the specialized brood pouches of *A. bifurca* where they are retained during incubation. However, if larval incubation is carried beyond a pelagic stage in *A. bifurca*, then the ability to locate a host is of no advantage unless the bivalve frequently outlives the worm or becomes separated from it. Larvae have not been observed in the Wellington Harbour plankton, but if there is no short pelagic stage, overcrowding would occur on the *Pectinaria* tube. Therefore, larvae probably leave the parent, and a short planktonic life supported by pelagic or post-pelagic host-finding behavior would be an adequate provision for dispersal of the species.

The experiments illustrated in this paper show that *Arthritica bifurca* is attracted to *Pectinaria australis* chemotactically by way of exhalant water currents from the tube worm, and that there is a direct orthokinetic response as the bivalves move closer to the host.

SUMMARY

1. The bivalve mollusk *Arthritica bifurca* (Webster), previously considered to be free-living, has been found in large numbers living commensally with the tubicolous polychaete *Pectinaria australis* Ehlers.

2. *Arthritica bifurca* is attached by several fine byssus threads to the outer surface of the head-end of the tube of *Pectinaria australis*, orientated vertically with

its anterior end directed downwards. Biological reasons for this commensal relationship are obscure.

3. Ecological observations on the *Pectinaria australis* population at Petone Beach, Wellington Harbour, suggest that the polychaete lives for only 12 or 18 months, and is subject to an extremely high mortality rate during growth and maturation and also after breeding in the spring. There is evidence for a fairly extended breeding period, and the population is probably replenished mainly during late summer by settlement of larvae at or near the high tide level.

4. Larvae of *Arthritica bifurca* are incubated by the parent at least to the shelled prodissoconch stage. A short planktonic larval life supported by pelagic or post-pelagic host-finding behavior is the probable means by which the commensal bivalve is dispersed.

5. Physiological experiments with live material established that *A. bifurca* is able to distinguish between sea water that has passed over the host and sea water which has not done so. The bivalves are attracted chemotactically to *Pectinaria australis* by way of exhalant water currents from the tube worm, and there is a direct orthokinetic response as the bivalves move closer to the host.

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